Devonian Vertebrates in Biostratigraphy

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Standards of precision in biostratigraphic dating and correlation of marine formations within the Devonian System now call for similar advances in the stratigraphy of non-marine formations. Vertebrates are amongst the fossils most commonly found in non-marine units but are very rare in the marine facies. Use of palynomorphs, macroplants and invertebrates and intensive study of interbedded marine and non-marine facies in all parts of the world are now urgent in clarification of Devonian world stratigraphy. The efforts of vertebrate palaeontologists are vital in this connection.

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INTRODUCTION

In several parts of the stratigraphic column vertebrates have become recognized as valuable biostratigraphic indices. Vertebrate evolution is comparatively rapid but the disadvantages of vertebrates in biostratigraphy are manifestly well known. Devonian vertebrate biostratigraphy is still in a relatively primitive state, being broadly confined to the continental facies. A notable 'pioneer' Devonian paper was by Gross in 1950 and from the most recent general statement (Westoll, 1979) a summary diagram has been prepared. Between these two mentioned dates Devonian invertebrate biostratigraphy has advanced significantly (House, Scrutton, Bassett, 1979). The International Commission on Stratigraphy, through its Subcommission on the Devonian System, is moving towards the adoption of international formal biostratigraphic definition of the (marine) Series and Stages within the System. So far it has agreed that

a) the base of the Middle Devonian is the base of the *P. partitus* conodont zone. This is approximately the base of the Eifelian stage (Heisdorf-Lauch boundary) in the Rhineland where the stratotype is at Wetteldorf

b) the base of the Upper Devonian is the base of the Lower *Pa. asymmetricus* zone which coincides with the base of the Assize de Frasnes in Belgium

c) while the existing stages of the Middle and Upper Devonian will not be discarded, the choice between the Lower Devonian stages of the Ardennes-Rhineland and those of Bohemia as the international standard has yet to be made. Pelagic fossils (especially microfossils) have been useful in this work but correlation of the marine with the non-marine facies lags behind. There is much evidence to suggest that spores and macroplant fossils will ultimately be of greatest value in this work, though there are dangers in the unquestioning use of spores alone.

In general, the broad recognition of Lower Devonian, Middle Devonian and Upper Devonian vertebrate faunas can be made, and faunas from the two higher Series are found in all continents except South America. Smaller biostratigraphic units based on vertebrates, however, are exceptional, and in the Lower Devonian the faunas tend to differ between four or five palaeobiogeographical provinces (Young, 1981).

As the examination of extensive and critical sections around the Lower/Middle and Middle/Upper Series boundaries has proceeded, it has become obvious that accurate correlation of marine horizons with non-marine is particularly wanting and that

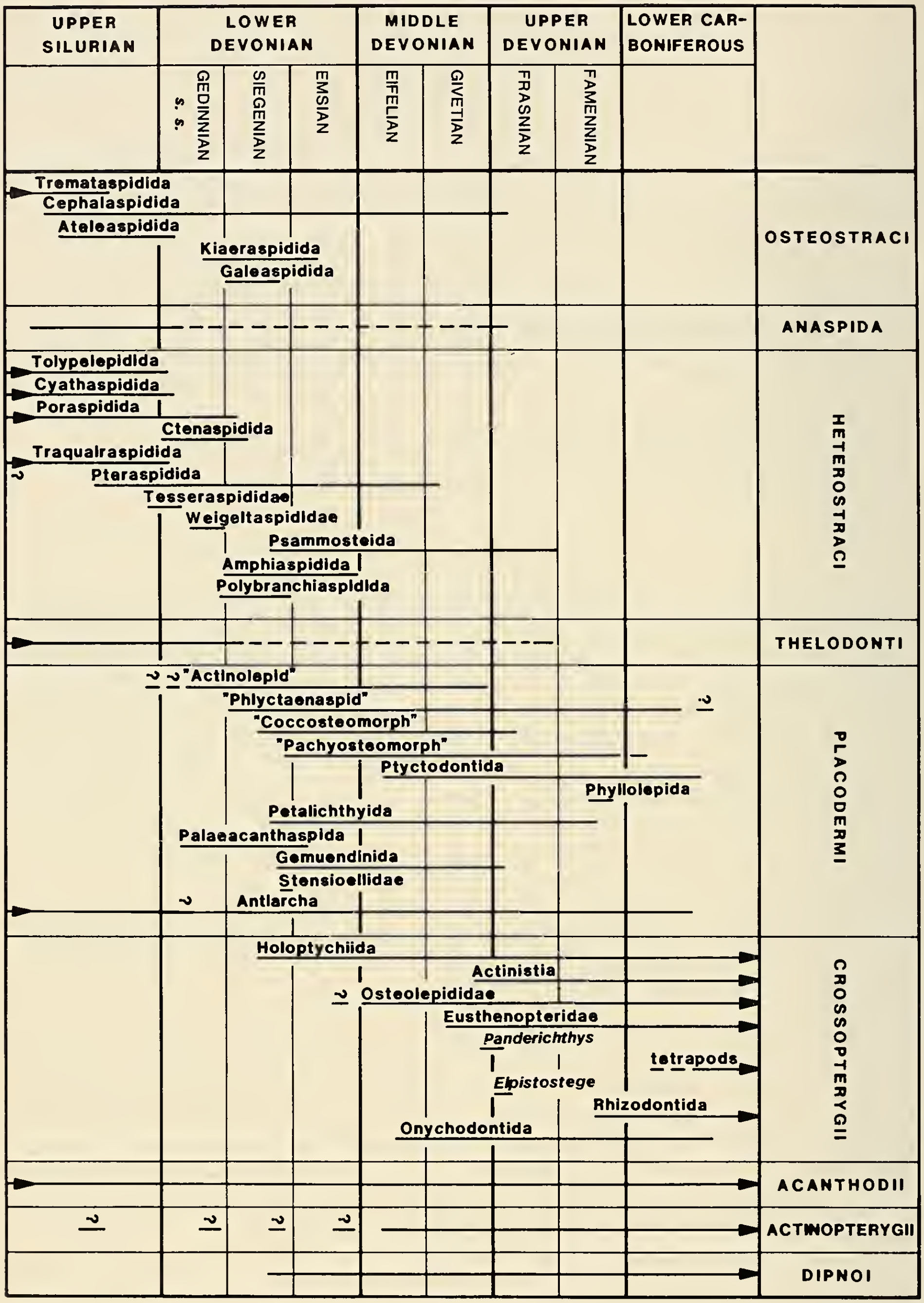

Fig. 1. A summary table of the ranges of vertebrate groups in the non-marine Devonian facies after Westoll (1979) and others.

vertebrate faunas are particularly scarce at those levels. Nevertheless good sections in the non-marine Devonian facies do exist and vertebrate successions within the series are known. This paper calls for efforts to be made to document the stratigraphic distribution of vertebrates and especially for the establishment of reference sections by which correlation from region to region and between facies may be made with greater confidence.

Old Red Sandstone Vertebrate Biostratigraphy, North Atlantic Area

Although attention has been given mainly to the detailed stratigraphic distribution of vertebrates, especially the ostracoderms, in the Old Red Sandstone outcrops of the North Atlantic area (Allen, Dineley and Friend, 1968; Young, 1981; Blieck, 1982) it is probable that other regions may provide better sections for detailed biostratigraphy and inter-facies correlation. China, parts of the Soviet Union and of Australia come to mind. Correlation between marine and non-marine facies in each region or province is the first important step to be achieved if possible and the correlation of non-marine formations and 'horizons' with those identifiable on an international biostratigraphic basis is to be preferred. This should in time allow correlation between different non-marine facies provinces as shown below.

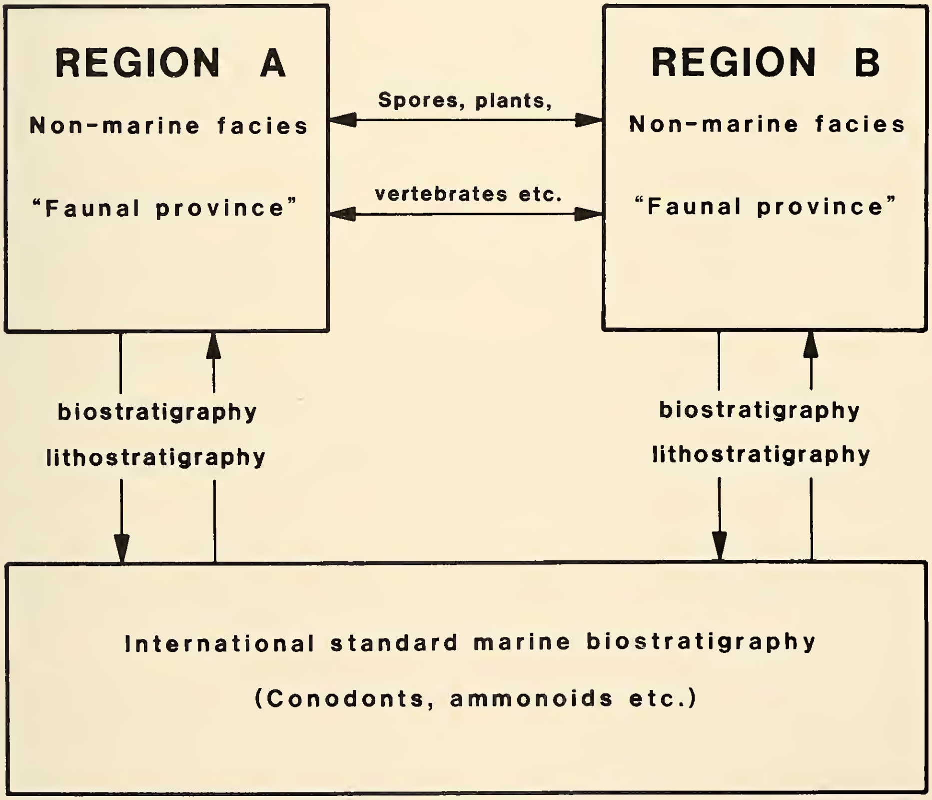

Fig. 2. Correlation between separate sedimentary basins or 'provinces' of non-marine deposits is unlikely to be achieved on the basis of lithostratigraphy and only achieved with uncertainty where there are few taxa in common. There is now a reasonably good basis of international biostratigraphy with which most non-marine Devonian facies may be correlated, given the presence of a few different fossil groups.

The North Atlantic region might be said to illustrate the point well. It includes formations from all three series of the System and where there are not actual unconformities between series the positions of those boundaries are difficult to define. Vertebrate remains are relatively common in the Lower Devonian of western Britain, Spitsbergen, eastern and northern Canada; in the Middle and Upper Devonian of Scotland, and Melville and Bathurst Islands, N.W.T. Canada, and Greenland. Other areas have yielded vertebrates in smaller numbers, others have yet to provide even a minimal number of identifiable taxa. Detailed modern studies in which systematic examination of stratigraphic sections with their vertebrate and palynological record are comparatively few. Of note are those in Wales and the Welsh Borderland (Ball, Dineley and White, 1961), Svalbard (Blieck, 1982a; Blieck and Heintz, 1979), E. Greenland (Friend *et al.,* 1973) and N.E. Scotland (Donovan, Foster and Westoll, 1973). Scattered valuable data have been recorded from many other areas, especially western Europe (Blieck, 1982b). Work on the succession in the Silurian-Devonian of the Canadian Arctic Islands (Elliott and Dineley, 1983) suggests further detailed correlation. For the Lower Devonian a number of 'zones' and 'horizons' have been designated and these are essentially assemblage or acme zones based on thelodont or heterostracan faunas. Material from Somerset and Prince of Wales Islands in the Canadian Arctic may allow zoning on the basis of a phylogenetic sequence of heterostraci originating at a pre-Devonian level. For the rest, phylogenetic sequences of vertebrates are lacking, though tentative phylogenies may be proposed. Continuous stratigraphic sections through the strata in which the assemblage zone fossil occurs in Britain are also wanting (Dineley, 1982). Formal establishment of a zonal sequence based upon unbroken stratotype sections throughout the Lower Devonian is not yet possible.

In the long-studied Middle Devonian of Caithness and the Orkney area a sequence of characteristic 'zones' and faunas has been distinguished by Westoll and his co-workers. (See also Donovan *et al.,* 1973; House *et al.,* 1977). The stratigraphic relationships of these 'zones' are established on the basis of excellent coastal sections, but there remain barren intervals of strata between the boundaries of the 'zones' themselves.

The Upper Devonian or Upper Old Red Sandstone formations of Scotland and Greenland have provided many data on vertebrate distribution and the Baltic-Russian platform outcrops of Middle and Upper Old Red Sandstone have also yielded a wealth of data that has been summarized by Mark-Kurik (1978) and other workers.

Correlation, and the dating, of these vertebrate-yielding formations with the local marine sequences proceeds largely by palynology. Correlation between the Atlantic area and other vertebrate 'provinces' is not so far advanced. While the standard Rhenish or Bohemian stages for the Devonian may be recognized universally and referred to stratotypes in Europe with increasing confidence, the condition of the stages proposed for the non-marine facies is much less satisfactory. A note on the British Old Red Sandstone stages in use may illustrate the point.

DOWNTONIAN Although the term was first used by Lapworth (1879) and later used by Peach and Horne (1899), it was employed for the lowest major division of the Old Red Sandstone in the Welsh Borderlands by King (1934) and White (1950) defined the stage by the incoming of *Hemicyclaspis* and its base in the stratotype sections at Ludlow by the base of the Ludlow Bone Bed. In terms of the marine Silurian-Devonian sequence this is now level with the base of the Pridoli stage, i.e. around the base of the *Monograptus ultimus* zone.

Recently Bassett, Lawson and White (1982) clarified the present status of the Downton Series as the fourth series of the Silurian System, thereby removing it from

		Series or Stage	Banks, 1980	McGregor, 1977	Richardson, 1974
CARBONIFEROUS		Tn 1b Tn 1a	?		*V. nitidus* *V. pusillites* *S. lepidophytus*
DEVONIAN	UPPER	FAMENNIAN	*Rhacophyton* Assemblage-zone VII		
		FRASNIAN	*Archaeopteris* Assemblage-zone VI		*L. cristifer* *optivus-bullatus*
	MIDDLE	GIVETIAN	*Svalbardia* Assemblage-zone V		*Triangulatus* *Densosporites devonicus*
		EIFELIAN	*Hyenia* Assemblage-zone IV	*devonicus-orcadensis* *velata-langii*	*Rhabdosporites langii* *Acinosporites acanthomammillatus*
	LOWER	EMSIAN UPPER	*Psilophyton*	*annulatus-lindlarensis* / *Grandispora*	*Calyptosporites biornatus-proteus*
		EMSIAN LOWER	Assemblage-zone III	*sextantii* *caperatus-emsiensis*	*Emphanisporites annulatus* *Dibolisporites cf. gibberosus*
		SIEGENIAN	*Zosterophyllum*		
		GEDINNIAN	Assemblage-zone II	*micrornatus-proteus*	*Emphanisporites micrornatus* *Streelispora newportensis*
SILURIAN		PRIDOLIAN	*Cooksonia* Assemblage-zone I	*chulus-?vermiculata*	*Synorisporites tripapillatus*

Fig. 3. Palynological and conodont zones and macroplant assemblages useful for international correlation in the Devonian System (after Banks, 1980, and others).

the Devonian System and formalizing its status. A description of the stratotype is given, parastratotypes designated and a correlation of the Downton Series with E. Canada and Europe given on the basis of invertebrates, vertebrates and spores. For all intents and purposes, the term Downtonian as a *stage* name should now be discontinued and reference to a Silurian Downton Series made instead.

DITTONIAN Based on his Ditton Series around Ditton Priors, Shropshire, this stage was designated by King (1934) as having at its base a *Cephalaspis* Sandstone (not identifiable elsewhere). Later practice has been to use the main *Psammosteus* Limestone

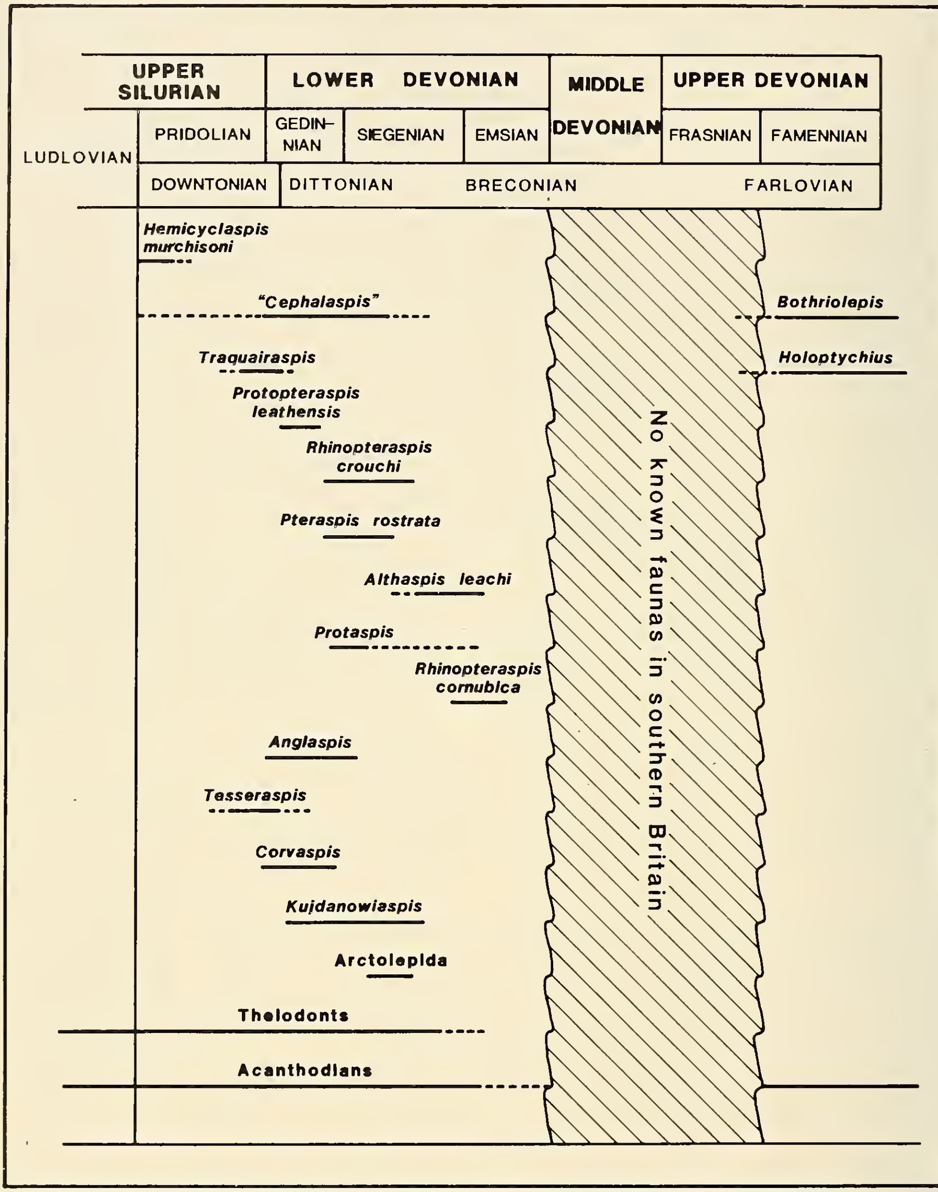

Fig. 4. Vertebrate 'zones' for the Lower Devonian of the North Atlantic province (after Dineley and Loeffler, 1976; Blieck, 1982).

as the mappable base, but to define the base of the stage (and hence the top of the Downtonian) as the base of the lowest bed yielding *Pteraspis (Protopteraspis) leathensis* (see White, 1950; Allen and Tarlo, 1963). Tarlo (1965) subsequently decided that the base of the *Monograptus uniformis* zone (the base of the Devonian System, McLaren, 1977) should occur at about the level of the Downtonian/Dittonian boundary. Direct

		N.E. SCOTLAND	E. BALTIC
UPPER DEVONIAN		*P. magnus*	*Plourdosteus*
MIDDLE DEVONIAN	Upper Caithness Flagstones Group	*Millerosteus minor*	*Pycnosteus tuberculatus*
		Asmussia murchisoniana	
		Dickosteus threiplandi	*Pycnosteus pauli*
	Lower Caithness Flagstones Group	*Palaeospondylus gunni*	*Pycnosteus palaeformis*
		Coccosteus cuspidatus	*Schizosteus striatus*
		Thursius macrolepidotus	*Schizosteus heterolepis*

Fig. 5. Vertebrate 'zones' for the Middle Old Red Sandstone of the Orcadian basin and a possible correlation with the Baltic area (after Donovan *et al.*, 1973, and others).

correlation has yet to be made between the graptolite and the vertebrate horizons but via the use of ostracodes a correlation has been suggested (Martinsson, 1967).

BRECONIAN The group of strata is defined as lying between the Dittonian and the Farlovian (Croft, 1953) and was used to include the Senni Beds with *Rhinopteraspis dunensis* and the overlying barren Brownstones (White and Toombs, 1948) in South Wales. This definition is unsatisfactory and the acceptance of a revised Breconian stage for the uppermost Lower Old Red Sandstone or its total abolition is overdue.

ORCADIAN This term has only been used informally for the Middle Old Red Sandstone and has its origins in the successions of Caithness and Orkney. It could be said to encompass the zones listed above but to what extent it is equivalent to the entire Middle Devonian Series cannot be stated.

FARLOVIAN This term (King, 1934; Ball, Dineley and White, 1961) has been used for the Upper Devonian in South Wales and the Welsh Borderland. At Farlow, Shropshire, the Farlow rocks rest unconformably upon Dittonian and Breconian strata and the fauna is neither distinctive nor well known enough to be of much biostratigraphic use.

All in all, these stages cannot be regarded as very satisfactory and only by careful redefinition and reference to specific stratigraphic sections can some be made 'respectable'. Nevertheless, they have been used successfully in broad correlation (see for example Obruchev and Karatajute-Talimaa, 1967). The Orcadian needs special study but the Farlovian should probably be discarded.

'Cosmopolitan' Lower Devonian vertebrates occurring in this and other provinces of Devonian marine and continental deposits include the thelodonts, various placoderm groups and early osteichthyes. Of these the thelodonts are proving to be the most widespread and may have the greatest biostratigraphic significance (Turner, 1973; Turner and Turner, 1974; Turner, Jones and Draper, 1981; Turner and Tarling, 1982).

Devonian Vertebrate Biostratigraphy Elsewhere

The work of Chinese specialists in fossil vertebrates and in Devonian stratigraphy has been important in recent years, not only in revealing the unique character of the early Devonian vertebrate faunas of China but also in establishing possible phylogenetic lineages of antiarchs (Pan, 1981) and in proposing stages for the extensive non-marine formations there. The work is based upon extensive field data, and palynological correlation with marine facies is improving. In detail, no doubt, revisions will have to be made, but progress appears to be systematic and encouraging. The Russian platform (Baltic area) Devonian has been studied for many years and the palaeontological record there of vertebrates and marine invertebrates is excellent. Summaries and overviews are now providing a wealth of data for particular intervals. Sorokin's (1978) monograph on the Frasnian stage and Lyarskaya's on Baltic Devonian Placodermi (1981) are good examples. In Central Asia and Siberia (Nalivkin *et al.*, 1973) palynological and palaeobotanical studies are being carried on especially in connection with the definition of the boundaries of the Middle Devonian and are important for the equation of continental vertebrate horizons (see e.g. Novitskaya, 1971) with the marine biostratigraphy (see Sokolov, Rzhonsnitskaya *et al.*, 1982).

In the western United States and Canada discoveries of Devonian vertebrates in marine formations or in beds intercalated with marine strata the ages of which are known in detail have recently been numerous (Gregory, Morgan and Reed, 1977). The affinity of some western American species with those from the Baltic area is striking and the intercalated conodont faunas in Nevada are of great importance.

In Australia Devonian continental facies are known to be widespread, especially those in the Middle and Upper Devonian. The stratigraphic distribution of the different vertebrate taxa is dealt with by other authors in the present symposium (see also Long, Turner and Kemp, 1983), and precise non-marine stratigraphic ranges for all known Devonian vertebrate species may be available in the forseeable future. Probably these ranges will be mirrored in Antarctic stratigraphy. Where possible, the identification of intercalated marine beds together with palynology and other studies in both facies will certainly assist in establishing a more detailed biostratigraphic correlation.

Discussion about the palaeontological basis of stages in continental facies has been minimal, but is now urgent. A consensus of opinion should not be hard to reach.

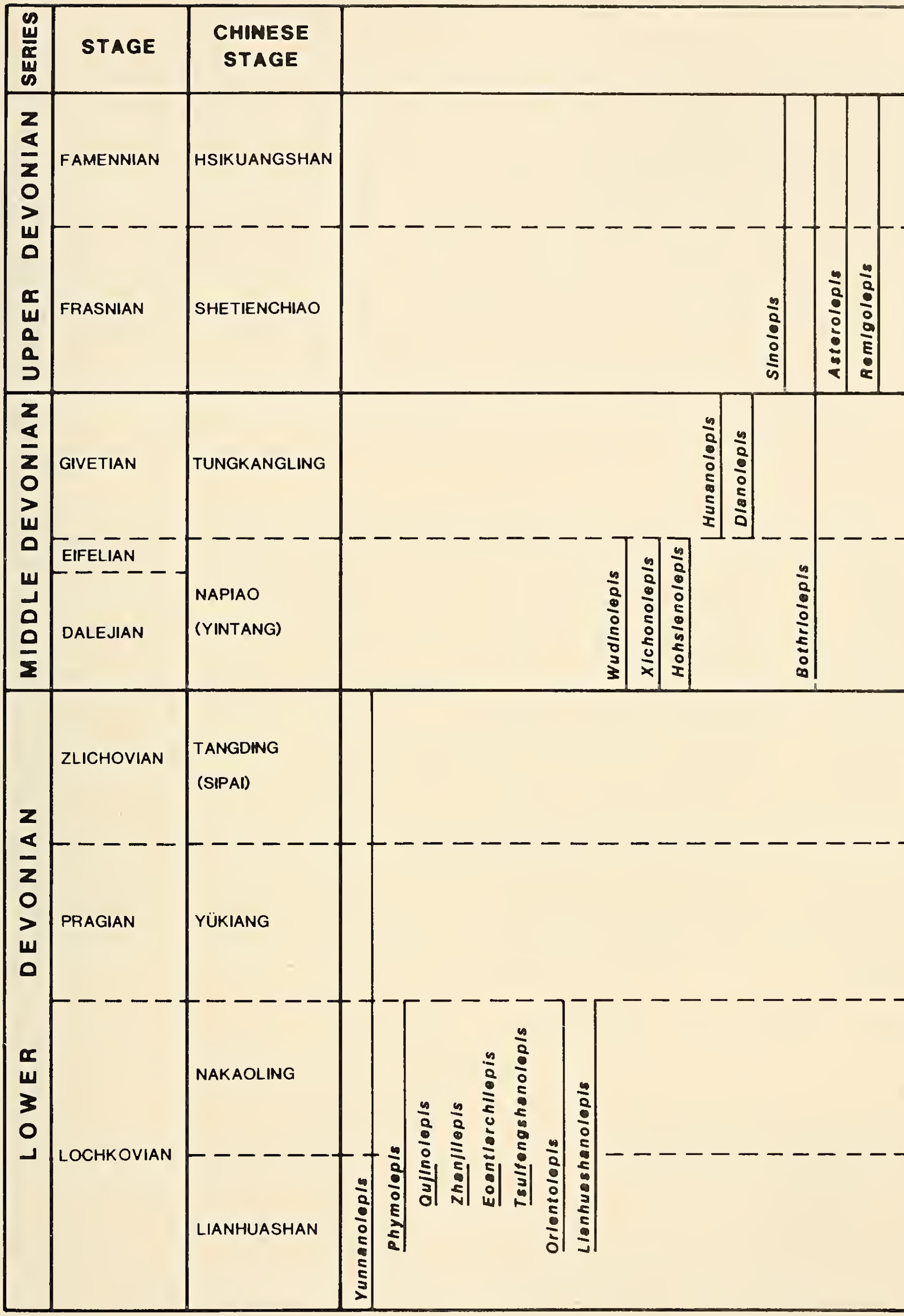

Fig. 6. Stages for the Qilianshan and Qujing (non-marine) facies types and the ranges of characteristic Antiarchi (after Yang, P'an and Hou, 1981; P'an, 1981).
Note that all genera except the three farthest to the right hand side are endemic and that only *Yunnanolepis* is known to reach the top of the Lower Devonian Series. The nature of the record at the upper and lower boundaries of the Middle Devonian is clearly very important and is a topic for special attention.

Conclusion and Proposal

In four of the five Devonian vertebrate provinces designated by Young (1981) there now exists a substantial mass of data that can be examined and assessed for the purpose of setting up successions of biostratigraphic units at 'horizon' or 'zonal' level. These units may also be assessed relative to successions of palynomorphs, macroplants or invertebrate fossils which allow comparison with local, and it may be hoped, the internationally-accepted criteria for Devonian Series and Stages. Local stages established for non-marine successions may be distinguished and be useful on a regional scale but, ultimately, correlation with a world-stratigraphic scale is necessary.

The value of such correlation is great not only in terms of palaeogeographical reconstructions but also in assessing the rates of geological change and organic evolution, migration, etc. In particular the chronology of early vertebrate endemism, migration(s) and of the extinction of particular groups may be revealed.

The evidence to establish good *zones based upon type sections* is less satisfactory but it does exist. To achieve such zonation in each province may require much more work and refined techniques generally regarded as those of ecostratigraphy must be employed.

It is urged that vertebrate palaeontologists and stratigraphers in the regions primarily concerned establish informal local working groups, linked if possible to existing working groups concerned with Devonian stratigraphy. They could most usefully draw attention to and study the best available type areas and putative type sections for vertebrate biostratigraphy. Co-operation with palynologists and palaeobotanists is essential. Correlation of designated type sections and stratotypes with local marine successions must be the aim followed by attempts at correlation with regional and international standard sequences. The liaison and co-operation of groups of workers — North American — W. European, Siberian — Central Asian, Chinese, Australian — Antarctic — with one another and with the Subcommission on the Devonian System is of course a direct and essential consequence. In due course an integration of the work of such working groups or of their representatives with that of the Subcommission would be advantageous. Meanwhile, the case for increasing local and international endeavour, using vigorous stratigraphic methods is now greater than ever before, and the results may be far-reaching. In this the vertebrate palaeontologist is an essential member of the group and he, or she, has perhaps the most to gain from its success.

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Note added at proof stage: At its meeting at Montpellier, France, on 23rd September, 1983, the Subcommission on Devonian Stratigraphy, set up a Working Group on the correlation of the marine with the non-marine facies of the Devonian, the present author to be convener of the Working Group.